#### MILLER, MELIACEAE

# THE GENERA OF MELIACEAE IN THE SOUTHEASTERN UNITED STATES<sup>1</sup>

# NORTON G. MILLER<sup>2</sup>

#### MELIACEAE A. L. de Jussieu, Gen. 263. 1789, 'Meliae', nom. cons.

# (MAHOGANY FAMILY)

Small to large trees [shrubs, or rarely sulfrutescent herbs]; new growth from terminal buds or from axillary buds, if axillary, then the branch apices dying back at end of growing season; bud scales imbricate [or absent], pubescent or not, deciduous; pith homogeneous [or with clusters of fibers]; new growth near leaf insertions with or without extrafloral nectaries. Leaves alternate, exstipulate, once or twice odd- or even-pinnate [trifoliolate, or simple]; spirally arranged [rarelv decussate]; trichomes of young leaves simple and hooked, glan-

<sup>1</sup>Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible through the support of National Science Foundation Grant BSR-8716834 (N. G. Miller, principal investigato), under which this account was largely prepared, and BSR-8716834 (N. G. Miller, principal investigato), under which this account was largely prepared, and BSR-8717333 (C. E. Wood, Jr., principal investigato). The 135th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. 39: 296-346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets []. The references that I have not verified are marked with asterisks.

Several hotanical colleagues helped in various ways in the preparation of this paper, particularly C. E. Wood, Jr., W. J. Crins, G. C. Tucker, I. A. Al-Shehbar, G. K. Rogers, T. J. Rosatti, B. G. Schubert, and B. T. Styles, all of whom provided information, perspectives on the taxonomic literature, and/or comments on a draft of the manuscript. I also thank Stephen A. Spongberg for his editorial review of the manuscript. The staff of the New York State Library, and especially Alta Baech, Senior Librarian, and of the Libraries of the Armold Arboretum and Gray Herbarium, Harvard University, gave prompt assistance with the sometimes challenging tasks of satusfying my pleas for literature that was hard to acquire. Specimens housed in the combined herbaria of the Arnold Arboretum and Gray Herbarium and the herbarium of the New York State Museum, as well as liquid-preserved materials gathered in Florida by Carroll Wood and collaborators, and a plant of *Switenia Mangeni* under cultivation in the Harvard University Herbaria Building were used in this study. Cheryl Tribley, Shirley Rabideau, and Barbara Nimblet efficiently prepared the typescript.

The illustration of Melia Azedarach was drawn by Arnold D. Clapman under the supervision of G. K. Brizicky and C. E. Wood, Jr. In Frouze I all drawings are of liquid-preserved specimens; a is from material collected by Wood and A. Strahler at Fort Meade, Florida; b and e are from plants collected north of Brooksville, Florida, by Wood, K. A. Wilson, and G. R. Cooley; and d-g are based on plants collected at Salem, Yirginia, by Wood. In Fioruse 2 all drawings are based on fresh (h=n) or liquid-preserved (a=g) material collected by D. Sturrock in West Palm Beach, Florida; a=g and n are by Rachel Wheeler (with dissections by Wood). In- me by Sue Sargent.

This paper is published as Contribution Number 654 of the New York State Science Service.

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© President and Fellows of Harvard College, 1990. Journal of the Arnold Arboretum 71: 453-486. October, 1990. dular, dendritic, or stellate [or peltate scales]; leaflets symmetrical or asymmetrical, serrate or entire, deciduous with rachis or not [rachis rarely winged, sometimes with an intermittently growing terminal "bud"]. Plants polygamous or monoecious for rarely dioeciousl; inflorescences axillary, large or small bracteate thyrses [panicles, or rarely spikes, sometimes cauliflorous or ramiflorous, or flowers epiphyllous], cymules 3-flowered, the terminal (firstopening) flower perfect or carpellate, lateral flowers staminate; staminate flowers deciduous after anthesis. Flowers regular (actinomorphic); in Melia perfect and staminate flowers similar at anthesis, in Swietenia staminate and carpellate flowers dimorphic. Sepals [2-4 or]5(6)[or 7], separate or fused basally and calyx then 5-(rarely 4- or 6-)lobed [or calvx circumscissile]. Petals [3, 4]5(rarely 6)[8 or 141 free for sometimes fused below to staminal tubel, in 1 for rarely 21 whorls, glabrous or pubescent abaxially, alternate with the sepals, the aestivation convolute, imbricate for contorted or valvatel. Stamens united into a cylindrical or urn-shaped [cyathiform] tube [or filaments free], tube fringed [or not] with [8 or 9]10(or 12) teeth, individual teeth deeply cleft or not; anthers [3-]10(12)[-23], [rarely septate], in onc [rarely 2] whorl[s], sessile on inside [or topl of tube [or with short filaments from top of tube], basifixed or dorsifixed. glabrous for pubescent], alternating with the teeth or seemingly opposite two narrow teeth, dehiscence introrse, connective short for sometimes greatly prolonged and filiform]; pollen [3- or] 4-colporate. Gynoccium syncarpous, the ovary superior [very rarely inferior], [3-](4)5 or 6[-15]-locular, each locule with 2 superposed ovules or with numerous ovules in 2 rows [ovules sometimes few and collaterall, the placentation axile [rarely parietal], ovules anatropous, nectariferous disc annular, entirely below the ovary or extending slightly upward, obscurely lobed and free from the ovary [or cyathiform, tubular, rarely a stipe supporting the gynoecium, or absent]. Ovary in perfect flowers pyriform and tapered into a long style, stigma rounded, scarcely wider than style; in carpellate flowers ovary globose, style short, stigma discoidal and nearly as wide as mouth of staminal tube [or obconical, globose-capitate, or 3-6-lobed]. anthers withered [staminodia rarely present]; in staminate flowers ovary narrowly pyriform, style abruptly differentiated and longer than in carpellate flowers, stigma discoidal, Fruit a drupe, endocarp 5- or 6-locular, keeled, usually one seed per locule [or endocarps separate, thin or thick walled] or a 5-locular capsule, septicidally [loculicidally] dehiscent from base [or apex], columella persistent, [or fruit a fleshy or leathery berry, or very rarely a nut]. Seeds retained within the endocarp or winged and dispersed after capsule dehiscence [commonly with a brightly colored arillode or sarcotesta]; cotyledons collateral, longer than broad or broader than long, embryo short, straight [or curved]. plumules minute or absent; endosperm fleshy, oily or more commonly thin and appearing absent; germination phanerocotylar or cryptocotylar. (Including Cedrelaceae R. Brown in Flinders, Voy. Terr. Austral. 2: 595, 1814, "Cedreleae": tribe Aitonieae Harvey in Harvey & Sonder, Fl. Capensis 1: 243. 1860 [Sapindaceae].) Type GENUS: Melia L.

A mainly tropical family of moderate size (50 genera, 550 species, according to recent monographic study; Pennington & Styles), with 14 genera (eight native,

six introduced) represented in the New World. Only Cabralea A. Juss. (one sp.), Ruagea Karsten (ca. five spp.), Cedrela P. Browne (seven spp.), Schmardaea Karsten (one sp.), and Swietenia Jacq. (three spp., one in our area) are endemic to the Western Hemisphere; Trichilia P. Browne (85 spp.; largely lowland tropical America, some species in Africa and a few in the Indo-Malayan region), Guarea Allamand ex L. (35 spp. in tropical America, five in tropical Africa), and Carapa Aublet (two spp.; tropical America and Africa) are disjunctly distributed among portions of the New and Old World tropics. Of the introduced genera only one species of Melia L., M. Azedarach L., is widely established in tropical and warm temperate parts of North and South America, including the southeastern United States.

Over the past 20 years a great deal of new and important information has been discovered about the taxonomy of the Meliaceae, mainly by botanists associated with the Commonwealth Forestry Institute, University of Oxford, England. Their studies have been wide ranging; those pertaining to generic concepts are summarized by Pennington & Styles in a lengthy paper that contains many original observations and new analyses and interpretations. In addition the family has been monographed for the *Flora Neotropica* series (Pennington, 1981), and many problems involving difficult species complexes have been clarified, in part aided by the recent availability of new and more adequate collections and a better understanding of the biology—especially the floral biology—of the family.

The Meliaceae, excluding the Ptaeroxylaceae J. F. Leroy, are a reasonably coherent group of monoecious, dioecious, or polygamous woody plants (generally trees), mostly with alternate, pinnate leaves and regular pentamerous flowers containing a staminal tube and a hypogynous nectariferous disc. Four subfamilies are recognized (Pennington & Styles), two of which are represented in our area. Subfamily Melioideae [Harms] (plants polygamous or dioecious, ovules 1 or 2, superposed or collateral, fruit a drupe, berry, or loculicidal capsule, seeds not winged, rays of wood usually 1 or 2 seriate) contains Melia Azedarach, a naturalized tree in our area, in tribe Melieae [DC.]. Six additional tribes accommodate genera represented in the neotropics, paleotropics, or both. Subfamily Swietenioideae Harms (plants monoecious, ovules usually many in two rows, fruit a septicidal capsule with a central columella, seeds winged, rarely otherwise, rays of wood generally 3-6 cells wide) includes Swietenia and eight other genera in tribe Swietenieae (A. Juss.) Spach,3 plus two additional tribes that include neotropical and/or paleotropical genera not represented in our area. In general the flowers of members of the Swietenioideae are small or

<sup>1</sup>Adrien de Jussieu in his "Mémoire sur le Groupe des Méliacesa" recognized two families, Méliaceae and Cedrelaceae, which he divided into groups of genera, providing a name for each group and Latin diagnoses but no designation of rank. Spach (Hist. Nat. Vég. Phan. 3: 161–205. 1834) used the rank tribe for De Jussieu's groups. The De Jussieu "Mémoire" was published in 1832 (1830 is the year on the title page of volume 19 of Mém. Mus. Hist. Nat. Paris in which the monograph was published, but the volume was issued in 1832; see Pennington. 1981, p. 4). The names and diagnoses of the new species and the subfamilial groups proposed by De Jussieu were, however, published in 1830 (Bull. Univ. Sci. Industr. Sect. 2 (Bull. Sci. Nat. Géol.) 23: 234–241) and also prior to 1832 in Linnaea 6(Li): 107–115. 1831. sometimes minute, in contrast to the larger, more showy flowers of members of the Melioideae.

Two monotypic subfamilies, Quivisianthoideae Pennington & Styles and Capuronianthoideae Pennington & Styles, accommodate genera endemic to the Malagasy Republic. The poorly known *Quivisianthus* Baillon in Grandidier has flowers similar to certain members of the Melioideae but differs substantially from them and other genera in the subfamily in having a loculicidal capsule and dry winged seeds. *Capuronianthus* J. F. Leroy is like members of the Swietenioideae in having a septicidal capsule, but it has naked buds, decussate leaves, and two superposed ovules (with two others aborting). Thus these subfamilies have certain characteristics of either the Melioideae or Swietenioideae, as well as some unique features.

Much is known about the chromosome cytology of the Meliaceae. About 100 species (of the ca. 550 species in the family) have been studied (Styles & Khosla), and this work has revealed greater variation in chromosome numbers (2n = 12 to ca. 360) than has been found in other woody, mainly tropical angiosperm families. Most counts are of mitotic figures from root tips (Styles & Khosla) although some counts are based on anther squashes. In many species the chromosomes are minute (0.5 to 3.5  $\mu$ m), even in cells of the root tip. Accurate determination of the higher numbers has been difficult because of staining problems (Datta & Samanta) and chromosome size. Most chromosomes have submedian to median centromeres. Polyploid series are present in some genera (e.g., Chisocheton Blume and Dysoxylum Blume of the Indo-Malayan region south to Australia and/or New Zealand). Within species variation in chromosome number (polyploidy, aneuploidy) is also known, for example, in Swietenia, Toona (Endl.) M. J. Roemer, and other genera. There is considerable disagreement about chromosome base numbers in the Meliaceae. Some authors have suggested x = 7 (Mehra *et al.*). Others cite evidence favoring two base numbers, x = 6, x = 7 (Khosla & Styles) or multiple base numbers, x = 9, 10, 11, 12, 13, 14 (Datta & Samanta). The most frequent haploid chromosome number in the family is 25. Chromosome numbers and karyotypes do not generally provide independent substantiation for subfamilies and tribes defined on the basis of morphology.

Flower morphology is extremely diversified in the Meliaceae. Characteristics of the androccium are particularly useful taxonomically at the generic level. The filaments are generally connate into a staminal tube (the shape of which may differ considerably among genera) or rarely are free. The anthers are inserted in the throat of the tube or at its summit, and they either are sessile or have short extensions of the filaments. Teeth occur along the distal edge of the tube, and the shape of these differs in taxonomically significant ways. The shape of the nectariferous disc, which is always located below the gynoecium, is also variable, as is the shape of the stigma. The patterns these structures present may be consistent within or among genera.

It has been suggested that the variability in floral structure may reflect adaptations for specific insect pollinators (White, in Pennington & Styles). However, the pollination biology of the family has been incompletely investigated. The flowers of some species are reported to be fragrant. This suggests insect

pollination, as does the uniform presence of floral nectaries. Flowers of *Guarea rhopalocarpa* Radlk. open at night and are probably moth pollinated (Bullock *et al.*). Moths were found to pollinate various species of *Guarea* and *Cedrela* in Costa Rica (Bawa *et al.*, 1985), and hymenoptera have been seen to effect pollen transfer in *Trichilia havanensis* Jacq. (White, in Pennington & Styles).

It has only recently been realized that genera characterized by perfect flowers are unusual in the Meliacea (Lee, 1967; Styles, who mentioned that this condition was restricted to *Turraea* L. and a few related genera; suspected also in some species of *Guarea* (Pennington, 1981)). What numerous authors in the past have described as perfect flowers are in reality either functionally staminate or functionally carpellate. In some cases (e.g., *Swietenia*) the carpellate and staminate flowers are conspicuously dimorphic, in others (e.g., *Melia*) the staminate and perfect flowers are superficially similar but can be told apart by inspection of the ovules, which appear aborted even in young staminate flowers. Poor staining quality of pollen or withered anther sacs characterize the functionally carpellate flowers, which only rarely have obvious staminodia.

It may be necessary to study plants in the field to ascertain whether a species is monoecious, dioecious, or polygamous. The reason for this, as Pennington (1981) points out, is that the staminate flowers are deciduous soon after anthesis, and they may not be present in herbarium specimens. In some dioecious species (e.g., *Trichilia Poeppigii* C. DC., of northwestern South America) not only are the flowers dimorphic, but the inflorescences are as well. A Costa Rican population of the dioecious *Guarea rhopalocarpa*, carefully followed for two years (Bullock *et al.*), showed complex patterns of flowering and fruiting in discrete episodes at irregular intervals during the study period, with two or three episodes per year per tree. Flowering occurred discontinuously over nine months of the year, and certain individuals flowered more or less at the same time. Trees with staminate or carpellate flowers were in about even proportion, but the number of staminate inflorescences during the census period was nearly always much greater.

Mechanisms of fruit and seed dispersal are also varied in the family. In many members of subfam. Melioideae the outer integument of the ovule becomes elaborated into a small or large sarcotesta, which can be rich in oils. The details of development of this structure are poorly known in most genera, but in some species it appears to originate from a specific part of the ovule. The meliaceous sarcotesta does not seem to be a proliferation of the funiculus, and therefore it is not exactly equivalent to an aril. In species with dehiscent fruits the sarcotesta is red or orange, and it contrasts with the black or brown unmodified seed coat. Such bright colors attract bird or mammal disperal agents.

Seed disperal in *Guarea glabra* Vahl, an understory tree producing abundant fruit, has been studied in Panama (Howe & De Steven). Seventy percent of the visits and 60 percent of the seeds removed involved four North American migrant birds (great crested flycatcher, Swainson's thrush, red-eyed vireo, and Tennessee warbler). Fruiting and the northward migration of these birds were synchronized. Of ten species of *Aglaia* Lour, studied by Pannell & Kozioł in Malaysia and Indonesia three had dchiscent fruits revealing seeds with a red sarcotesta (bird-dispersed), and seven had indehiscent fruits and seeds with a

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yellow, white, or translucent sarcotesta (five of these were primate-dispersed). More lipids were present in sarcotestas associated with bird dispersal; the coverings of the primate-dispersed seeds were gelatinous, low in lipid content, and high in sugars.

Bats are likely to disperse the fleshy fruits (and endocarps) of *Azadirachta indica* A. Juss. in West Africa (Ayensu) and perhaps elsewhere in the tropics. Fruits of *Meila* Azedarach are eaten and dispersed by birds in the United States and by birds and fruit bats in South Africa (White, 1986). Seeds of *Carapa guianensis* Aublet are eaten by rodents, monkeys, and wild pigs, which may be agents of dispersal (White, 1983). The buoyant seeds of this species, which prefers swamp forests in at least part of its range, are transported by water *(ibid.)*. In Amazonia several kinds of fish have been observed to eat the seeds of *C. guianensis*, but the seeds appear to be destroyed in the process (Gottsberger). Wind is the presumed dispersal agent for those species (mainly members of subfam. Switetnioideae) with dry, winged seeds.

Published morphological and anatomical studies of the Meliaceae have dealt mainly with wood anatomy and aspects of vegetative structure that are unusual in seed plants.

The early investigations of Kribs and of Panshin into the secondary xylem of representatives of the family yielded character sets that for many years were thought to be diagnostic for genera. However, wood of about one-half of the known species of Meliaceae has now been examined (Pennington & Styles), and some of the conclusions drawn by Kribs and Panshin are no longer tenable. Few genera of the Meliaceae can be distinguished on the basis of wood anatomy alone, but anatomical characters sometimes correlate with other morphological ones in taxonomically significant ways. Wood provides characters (e.g., fibers septate, terminal bands of apotracheal parenchyma absent vs. fibers nonseptate, apotracheal parenchyma present) that are helpful in delimiting subfamilies, and within the Melioideae in placing genera in tribes.

Leaves (as well as the bark and secondary xylem) of many Meliaceae have secretory cells. In leaves they are located in the mesophyll and with back lighting are visible as translucent dots. (Secretory cells are evidently lacking in Melia Azedarach and Swietenia Mahagoni, however.) The pinnate leaves of species of Guarea are unusual (Skutch) because they exhibit intermittent, indeterminate growth from a crozicr-like "bud" at the rachis apex, which remains meristematic. On the basis of anatomy and development such "leaves" are leaf homologs, although in their continuous growth (including increases in secondary xylem thickness) they are analogous to branches (Steingraeber & Fisher). Experiments performed by Fisher showed that leaflets in G. Guidonia (L.) Sleumer exhibited either a "sun" or a "shade" morphology and that within a given leaf the expression of one form or the other was plastic and related to whether the leaflets were initiated in the shade or in the sun. Leaves of G. rhopalocarpa are estimated to be 7-11 years old at abscission (Skutch). Such indeterminate leaves are also found in species of Chisocheton, a few species of which also have fewflowered, epiphyllous inflorescences. Vascular bundles supplying such inflorescences arise from the stele of the rachis with no evidence that the bundles are adnate to the rachis vasculature (Mabberley, 1979).

Basal leaflets in some Meliaceae are modified into stipule-like structures that are appressed to the leafbase-stem junction. The point of attachment is, however, the leaf rachis. Pseudostipules of varying form occur in species of *Trichilia* (Pennington, 1981), and they are known also in some other families of the Rutales (e.g., Sapindaceae; Weberling & Leenhouts). Sac domatia occur on the abaxial surfaces of leaves of *Dysoxylum Fraseranum* Benth. of Australia (Metcalfe & Chalk, 1979).

The palynology of the Meliaccae has been summarized by Pennington & Styles on the basis of studies of about two-fifths of the species in the family, including representatives of all genera. The family is stenopalynous, with little variation from the basic pattern (pollen subprolate or prolate-spheroidal, 3- or 4-colporate, psilate, sometimes verrucose) among genera once included in the Meliaccae, for example *Flindersia* R. Brown in Flinders to the Rutaceae and *Ptaeroxylon* Ecklon & Zeyher (which has neither meliaccous or rutaccous pollen) to the Ptaeroxylaccae (with *Cedrelopsis* Baillon). *Turraea* and allied genera (pollen generally oblate-spheroidal, 3-colporate, exine scabrous to verrucose) are the most disparate elements in the family palynologically. Pollen is of limited value in defining genera.

Chemotaxonomic studies of the Meliaceae have focused largely on the distribution and systematic significance of limonoids, a group of oxidized triterpenes otherwise known to occur in the Rutaceae and Cneoraceae. These secondary metabolites impart a bitter taste to the plant tissues in which they occur. A mixture of limonoids is present in most species, and different limonoids may be present in different parts of a plant (Taylor, 1983). Sometimes limonoids occur in only one plant organ. Only the most highly oxidized limonoids appear to be significant taxonomically. Various kinds of limonoids are partitioned in mostly nonoverlapping patterns among the Meliaceae, Rutaceae, and Cneoraceae, and within the Meliaceae between subfamilies Melioideae and Swietenioideae, but less clearly among the tribes recognized by Pennington & Styles. Melia and Azadirachta A. Juss. (both in tribe Melieae) have many limonoids in common, although Azadirachta has some that are lacking in Melia (Taylor, 1983). Alkaloids are reported from only five members of the Meliaceae (Mester), and coumarins are known in relatively few genera (Gray). Flavonoid chemistry has not been much used as a chemotaxonomic tool in the family (Harborne), and it is unclear how much potential it has.

The paleobotanical record of the Meliaceae consists of pollen, leaves, seeds, and fruits, mainly of Tertiary age. A few Cretaceous fossils have been attributed to the family (e.g., Graham, 1962). Structurally preserved wood from the Tertiary of Europe and North Africa is similar to that of the extant genera *Carapa*, *Entandrophragma* C. DC., and *Lovoa* Harms (Louvet, 1973, 1975; Mädel; Selmeir, 1983, 1987), and these occurrences are cited as examples of tropical or subtropical elements in pre-Quaternary paleofloras of the Mediterranean Basin region. *Cedrela* is represented by leaves, fruits, and pollen in the Eocene and Miocene floras of the western United States (MacGinitie; MacGinitie *al.*). Dispersed pollen of *Cedrela* and/or *Guarea* has been recovered from Oligocene and Miocene sediments in the Caribbean Basin (Graham & Jarzen; Graham, 1977). These occurrences suggest possible migrational tracks and temporal limits for the migration of neotropical plant elements occurring in the Tertiary paleofloras of the southeastern United States. The absence of palynological diversification and distinctive pollen types in the Meliaceae may limit how much information can be obtained from studies of dispersed fossil pollen.

Most members of the Meliaceae are forest trees, usually reaching the canopy or subcanopy, but sometimes only the understory. In the Neotropics the family is especially well represented in nonflooded lowland rain forest (terra firma) and in seasonally flooded lowland forest (várzea). Various genera are also represented in montane forests and sometimes in the cloud forests of central and northern South America. Certain species grow on drier sites, especially in the West Indies where species of *Trichilla, Guarea*, and *Cedrela* occur on dry (sometimes mesic) soils over limestone hills. *Xylocarpus granatum* Koenig and *X. mekongensis* Pierre, are mangroves, occurring in parts of the area from East Africa to tropical Australia and Polynesia (Tomlinson).

The family is of considerable commercial importance, primarily as a source of valuable timbers that are used to make high quality furniture. *Khaya A*, Juss, African mahogany, species of *Swietenia*, the true mahoganies, and species of *Entandrophragma* of tropical Africa yield perhaps the most valuable hardwood lumbers. A limonoid, azadirachtin, extracted from the seeds of *Azadirachta indica* A. Juss., neem tree, has elicited much interest as a growth inhibitor and an antifeeding agent against insects. Azadirachtin is presently under study for possible use in the control of insects that cause damage to food and other crop plants (Schmutterer & Ascher). Oil is extracted from seeds of species in a number of genera (Vaughan). Fruits of *Lansium parasiticum* (Osbeck) Sahni & Bennet (*L. domesticum* Jack), langsat, and *Sandoricum Koetjape* (Burm. f.) Merrill, santol, are eaten in Southeast Asia. The former is considered to be one of the best fruits of the Malayan region (Popenoe).

The Meliaceae are placed in the Rutales (Dahlgren et al., Takhtajan, Thorne) or Sapindales (Cronquist), both of which are variously circumscribed. There is general agreement, however, that these orders are allied and form a distinct evolutionary line, linked directly to magnolioid ancestors (Meeuse). Phytochemical markers (triterpenes), in addition to morphological criteria, indicate close evolutionary relationships among the Meliaceae, Simaroubaceae, and Rutaceae. Limonoids are known from the Meliaceae and Rutaceae, whereas quassinoids, which are biochemically derived from them, are restricted to the Simaroubaceae (Seigler), suggesting that the Simaroubaceae are advanced, at least in this character.

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## MILLER, MELIACEAE

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# Key to the Genera of Meliaceae in the Southeastern United States

General characteristics: Small to large trees; leaves alternate, exstipulate, once or twice odd-pinnate or even-pinnate; plants monoecious or polygamous; inflorescences axillary thyrses; flowers perfect, staminate, or carpellate (if only staminate and carpellate, then dimorphic), regular, pentamerous; sepals free or fused basally; petals free; stamens hypogynous, united into a fringed tube, or tube ending in deltoid teeth, anthers sessile; gynoecium syncarpous, 5-locular, stigma rounded, as wide as the style, or stigma discoidal, wider than style; ovules two, superposed, or many in 2 rows; fruit a drupe or a septicidal capsule splitting from base to apex; seeds remaining in endocarp or seeds free and winged.

# Subfam. MELIOIDEAE [Harms in Engler & Prantl, Nat. Pflanzenfam. III. 4: 267. 1896.]

# 1. Melia Linnaeus, Sp. Pl. 1: 384. 1753; Gen. Pl. ed. 5. 182. 1754.

Small [to large] trees [or shrubs]; branch apices dying back, new growth initiated from axillary buds; bud scales stellate pubescent. Leaves deciduous, once to twice, rarely thrice, odd-pinnate, a pair of glands (extrafloral nectaries?) located on new branches near leaf insertions; young leaves with a mixture of dendritic (or stellate) hairs and simple, hooked hairs; leaflets petiolulate, mostly symmetrical at base, acuminate, serrate. Plants polygamous; inflorescences borne in the axils of the early leaves, terminal flower of cymule perfect, lateral flowers staminate; perfect and staminate flowers similar at anthesis. Sepals 5(6?), mostly free. Petals 5(6?), weakly [or strongly] pubescent abaxially, alternate with the sepals. Staminal tube cylindrical, outer surface smooth or with linear appendages, inner surface with long hairs, tube 20(24?)-toothed; anthers 10(12?), sessile, basifixed, inserted inside the tube opposite pairs of teeth, as long as the teeth and bent inward over the stigma at anthesis, connective slightly prolonged; pollen ± prolate, exine smooth to slightly scabrate. Ovary 5- or 6locular, each locule with 2 superposed, anatropous ovules, style long-cylindrical, ending in a hemispherical stigma (style head) with five or six inwardly bent lobes [or lobes erect]; nectariferous disc annular, obscure, entirely below the ovary. Fruit a  $\pm$  globose [or ovoid] drupe, endocarp spheroidal [or narrowly ellipsoidal], keeled, 5- or 6-locular, or locules fewer by abortion; one, rarely



FIGURE 1. Melia. a–g, *M. Azedarach:* a, inflorescence and leaf, × ½; b, flower, × 3; c, staminate flower in partial vertical section (pctals and two sepals removed), showing gynoecium, nectariferous disc, staminate lube, appendages, and anthers, × 4; d, fruit (drupe), showing scars of staminate flowers on pedicel, × 1; e, fruit in diagrammatic cross section, showing 6-locular stone, 2 locules without seeds, endosperm stippled, embryos with 2 or 3 cotyledons, × 2; f, stone, from side, × 2; g, stone, from above, × 2.

two seeds per locule. Seed coats thin, brown; embryo ellipsoid, cotyledons flat, longer than broad, plumule minute; endosperm conspicuous, fleshy, oily. LECTOTYPE SPECIES: *M. Azedarach* L.; see N. L. Britton, N. Am. Trees 593. 1908. (Ancient Greek name for manna ash [*Fraxinus Ornus* L.].)—CHNABERRY.

A small genus indigenous to temperate, subtropical, and tropical regions of Asia and Africa, with one species, *Melia Azedarach*, chinaberry, China tree, pride of India, Carolina mahogany, 2n = 28, introduced into the Americas where it is now widely naturalized. The original range of *M. Azedarach* may be impossible to ascertain because the species occurs throughout a large part of warm-temperate and tropical Asia. Hiern (in Hooker) noted that *M. Azedarach* maximut in the sub-Himalayan tract, alt. 2–3000 ft."; Rechinger reported that *M. Azedarach* was spontaneous in the western Himalayas. Other authors (e.g., Coode & Cullen) concluded that its native range encompasses portions of the area from Nepal, India, Burma, and southern China, through parts of the Malay Archipelago to New Guinea, the Solomon Islands, and tropical Australia (see discussion that follows).

The introduction of *Melia Azedarach* into the United States is credited to André Michaux, who is said to have grown it in his garden near Charleston,

South Carolina, in the late eighteenth century. At the close of the second decade of the 1800's, F. A. Michaux reported that *M. Azedarach* had become abundant in coastal areas of the southern United States, and, about the same time, Elliott, in reference to South Carolina and Georgia, wrote that it was "perfectly naturalized" and "springing from seed in cultivated land and around enclosures." It is now widely grown and self-seeding throughout our area except in the mountains. Mabberley suggested that plants in North America seemed to have at least two distinct origins, viz. from Indian plants via the Middle East and from Chinese plants via Japan.

The cultivar 'Umbraculifera', Texas umbrella tree, 2n = 28, with a dense, flattened crown of foliage and the main branches radiating from the trunk like the supports of an umbrella, was first observed in Texas (where it may have originated). Most of the naturalized trees are of a much more open form. The Texas umbrella tree is widely planted in the southeastern United States.

Propagation of *Melia Azedarach* for horticultural purposes is from seeds or cuttings. The seeds germinate while they are still enclosed in endocarps, and one fruit may produce up to four seedlings. Germination percentages are usually high. Precocious flowering (sometimes even in the seedling stage) has occasionally been observed (van Steenis).

The circumscription of Melia is uncertain. Most authors state that the genus consists of 15 or fewer species, but it may actually contain about five species (Pennington & Styles, family references), or probably even a smaller number. Jacobs emphasized several important differences between Melia and Azadirachta A. Juss., which are sometimes treated as congeneric. The latter consists of two species, A. indica A. Juss. (M. Azadirachta L.), neem, a tree cultivated throughout India and held sacred by the Hindus, and A. excelsa (Jacob) Jacobs of the Indo-Malayan region. Some of the characters that distinguish Melia and Azadirachta are: leaves twice- or thrice-pinnate vs. once-pinnate; large extra-floral nectaries(?) near petiole bases, one pair (bth circular) vs. two pairs (one pair circular, the other linear); ovary 4–8-locular vs. 3-locular; style broad, stigma 4–6-lobed vs. slender and 3-lobed; and ovules superposed vs. collateral. However, Corner (family references) questioned whether Azadirachta, Melia, and Cipadessa Blume have been distinguished satisfactorily. He also mentioned that seeds of species of Melia and Cipadessa are similar.

Flowers and fruits of *Melia Azedarach* have been illustrated and described repeatedly. Less well-known species of *Melia* are included in various standard floras and other works that treat tropical or subtropical Asia or Africa. While numerous names exist for the considerable morphological diversity presented by the Asian plants, Mabberley concluded that only one polymorphic species, *M. Azedarach*, exists in that region. He proposed an informal infraspecific classification for *M. Azedarach* that consists of three categories, wild plants (incl. *M. dubia* Cav., *M. composita* Willd, *M. australasica* A. Juss., and other synonyms), Chinese cultivars (*numerous* synonyms). Many of these names have been used in floras or to document phytochemical or other investigations into the biology of *Melia*. The two groups of cultivars originated in different parts of Asia through selection for desirable horticultural qualities.

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Wild plants of *Melia Azedarach* occur in forests in an area including India and southern China, southward through the Indochinese Peninsula, parts of Malesia to New Guinea and tropical Australia, where they sometimes are large trees (to 40 m). Wild plants, which have larger leaflets (to 6 cm long) and smaller flowers, are evidently not hardy in cool-temperate regions. In contrast, plants naturalized or cultivated in temperate regions have smaller, serrate or lobed, usually glabrous leaflets and large bluish, pink, or white flowers. The chinaberry of the southeastern United States is presumably partly derived from plants introduced into Europe from the Middle East, which in turn are believed to have come at least as early as the 9th century B.C. from plants of Indian origin (Mabberley). Cultivars selected in Japan (from putative Chinese stocks) have been a second source of introductions into European and North American horticulture.

A name often applied to Mabberley's concept of wild plants of *Melia Azeda*rach is *M. dubia* Cav.; flowering and fruiting specimens so-named in the herbarium of the Arnold Arboretum are markedly distinct from *Melia Azedarach* as it is represented in the Southeast. Mabberley has added *M. dubia* and several other names to the synonymy of *M. Azedarach*, citing his inability to correlate differences in flower color and leaf characters with geography. It would be interesting to know if the "wild" plants are reproductively isolated from those in cultivation, in view of the fact that hybrids are known among at least some of the cultivars.

Melia Azedarach is widely naturalized in Africa, and one or perhaps two other species appear to be indigenous to that continent. Melia Bombolo Welw. is reported from West Africa (Sénégal, Gabon, Democratic Republic of the Congo, and Angola; Staner & Gilbert) and M. Volkensii Guerke from tropical East Africa (Uganda; Gürke). The relationship between these species and M. Azedarach s. l. is unclear. The genus obviously needs monographic study.

The sole representative of the genus in the Southeast, Melia Azedarach, is reported to be polygamous on the basis of observations of trees growing in Taiwan (Lee, Styles (1972), family references). Individual cymules in an inflorescence are mostly three-flowered dichasia in which the terminal flower is perfect (and the first to open) and the two lateral flowers are staminate. Perfect and staminate flowers can be followed by observing the pattern of fruit set. My examination of herbarium specimens collected in the Southeast revealed that fruits are usually at the ends of pedicels that bear opposite scars (which represent the places where the staminate flowers were attached). Polygamy should be confirmed in our area by observations of plants in flower.

Plants of *Melia Azedarach* have many uses, although the species is not of great commercial importance. The wood has been used in cabinets, furniture, and cigar boxes, and in the manufacture of fiberboard. Pulp from the wood has been made into various kinds of paper in India. Styles & Khosla (family references) consider *M. Azedarach* to be a "species of enormous forestry potential," and report that a program to improve the species genetically is under way in Argentina.

A decoction of bark from the roots is reputed to be an effective vermifuge, probably reflecting the presence of vanillic acid (Chiang & Chang). Other parts of the plant are also used occasionally in folk medicine. The seeds contain about 40 percent oil. The endocarps are sometimes strung as beads, for example, in rosaries. A triterpenoid, azadirachtin, originally isolated from the fruits of *Azadirachta indica*, but also found in the fruit of *M. Azedarach* (Morgan & Thornton), inhibits feeding in desert locusts (*Schistocera gregaria*). Other kinds of insects are repelled by extracts of the plant. Fermented fruits of *M. Azedarach* (Maberley).

Fruits and leaves of *Melia Azedarach* are reported to be poisonous to humans and certain domestic animals (Carratala, Kwatra *et al.*). However, the poisonous principle has been elusive. A toxic alkaloid, tazetine, has been found in the bark and fruit (Morton, family references), and the presence of an alkaloid, azedarine, is mentioned by Carratala. The work of Morrison indicated that the toxicity of the fruit derives from an unidentified alkaloid, which acts in concert with a resin. However, Schulte and coworkers did not detect toxic substances in the fruit sof *M. Azedarach*. Oelrichs and colleagues isolated four limonoids (meliatoxins) from the flesh of fruits from trees in Queensland. These proved toxic to pigs and mice in clinical trials.

Birds and fruit bats play a role in the dispersal of *Melia Azedarach* (White, 1986). In North America the robin (*Turdus migratorius migratorius*) is reported to eat quantities of the fruit (Beal, Elliott).

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#### Subfam. SWIETENIOIDEAE Harms in Engler & Prantl, Nat. Pflanzenfam. III. 4: 267. 1896.

## 2. Swietenia Jacquin, Enum. Syst. Pl. Ins. Carib. 4, 20. 1760.

Small to large trees; bark dark brown, shallowly fissured; scales of terminal buds glabrous. Leaves even-pinnate (rarely odd-pinnate), apex of rachis aborting; young leaves with numerous scattered glandular hairs and a few long, simple hairs: leaflets petiolulate [or sessile], oblique at base, lower part of lamina of each narrower than upper, short [to long] acuminate, entire; leaflets usually deciduous before rachis. Plants monoecious; inflorescences borne on new growth; terminal flower of cymules carpellate, lateral flowers similar, calyx of 5 (rarely 4 or 6), convolute in bud, entire or ciliate, otherwise glabrous. In staminate flowers the stamen tube urn-shaped, 10 (rarely 12)-toothed; anthers 10 (or 12), dorsifixed, inserted at a position below the stigma, alternating with the teeth; pollen spherical, ± psilate, margins of colpi thickened; ovary narrowly pyriform. (4)5(6)-locular, ovules rudimentary, style long, stigma narrower than

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mouth of tube; nectariferous disc annular, obscurely lobed, extending slightly above the insertion of the ovary. In carpellate flowers stamen tube urn-shaped, anthers small and withered, inserted above the stigma, anthers and teeth of stamen tube ± flexed over stigma at anthesis, ovary globose, (4)5(6)-locular, each locule with numerous anatropous ovules in 2 rows; placentation axile; style short, stigma as broad as mouth of stamen tube, discoid, indistinctly 5-rayed, stigmatic surface on lower side; nectariferous disc annular, obscurely lobed, extending slightly above the insertion of the ovary. Fruit a 5-locular capsule, dehiscing septicidally from the base [or apex and base or from the middle to the ends], pericarp 2-layered, the woody outer layer separating first, 5-ridged columella persistent. Seeds large, in 2 rows, winged, attached by the funiculus near the apex of the axis; wing mostly elaborated from outer integument, weakly [or strongly] aerenchymatous at base and around seed; inner seed coat thin; embryo transversely elliptic, located at the bottom of the seed below the wing, radicle oriented perpendicularly to the long axis of the seed and to the position of the micropyle, cotyledons broader than long, plumule inconspicuous; endosperm very thin, inconspicuous, oily. Type species: S. Mahagoni (L.) Jacq., the only one included in the genus when it was established by Jacquin. (Named in honor of Gerard von Swieten, 1700-1772, Dutch physician and botanist, who worked in Vienna during the last third of his life and who was instrumental in the establishment of the botanic garden at Schönbrunn and the University of Vienna.]-MAHOGANY, CAOBA.

Three species of tropical and subtropical America; one, Swietenia Mahagoni, West Indian mahogany, native in our area only at the southern end of Florida (Monroe and Dade counties, including the Florida Keys), but hardy northward in Florida. Otherwise, it is indigenous to the islands of the western and northern Caribbean region (Greater Antilles, Bahamas) but evidently was introduced in Puerto Rico, the Virgin Islands, and the Lesser Antilles (Little; Little & Wadsworth, family references). However, the exact extent of its native range is not known because this species was planted extensively, probably beginning in the 1700's, and some populations represent escapes from cultivation. Indeed, this important tree has been introduced throughout the tropics as a source of timber and as a shade tree. It seeds freely, and isolated mature trees are sometimes surrounded by numerous seedlings, as, for example, in the Lesser Antilles (Howard).

Swietenia Mahagoni is allopatric with S. macrophylla King, Honduran mahogany, known from Mexico and Central America (Veracruz and Chiapas, Mexico, and Belize south to Penama) and South America (Colombia and Venezuela and disjunct to Peru, Bolivia, and Brazil), and S. humilis Zucc., restricted to the Pacific slope of Mexico (Sinaloa southward), Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica. Swietenia macrophylla and S. humilis are sympatric in parts of Mexico, Guatemala, and Costa Rica (Lamb, 1966; Styles in Pennington, 1981, family references), but detailed studies of co-occurring populations evidently have not been undertaken. Putative, spontaneous hybrids between open-pollinated trees of S. macrophylla and S. Mahagoni, S. humilis and S. macrophylla, and S. humilis and S. Mahagoni have



FIGURE 2. Switemia. a–n, S. Mahagoni: a, inflorescence, × 1; b, staminate flower, × 5; c, same, with one sepal, petals, and part of staminal tube removed to show nectariferous disc and nonfunctional gynoecium, × 10; d, ovary of staminate flower in diagrammatic cross section, showing rudimentary ovules, × 12; e, carpellate flower with petals and part of staminal tube removed, showing gynoecium, disc, and rudimentary anthers, × 10; f, ovary of carpellate flower in diagrammatic cross section, showing ovules and placentation, × 12; g, inflorescence with very young fruit, and showing scars of staminate flowers, × 1; h, lealy branch with mature fruit, × ½; i, stages in opening of fruit, × ½; k, axis of fruit (columella) with seeds after fall of woody valves, × ½; H, ridged columella with seeds, radicle at left, cotyledon wider than long and extending above and below the position of radicle, cotyledons strongly coherent (second cotyledon not visible), × 2.

been recognized either in plantations of the parental species or in areas of sympatry (Whitmore & Hinojosa). The hybrids present various morphological traits that are intermediate between the parents, but detailed studies of progeny resulting from controlled crosses have not been undertaken to confirm these observations. Only in Taiwan have crosses between a tree of *S. macrophylla* (pollen parent) and *S. Mahagoni* been performed (Lee, 1968). The stomatal length to width ratio and leaflet size in the hybrid seedlings were in general intermediate between measurements of these features in seedlings from seeds produced through the self-pollination of flowers on the parental trees. Chromosome numbers of the plants used in this study were not determined.

The three species of Swietenia differ in a combination of traits, including vegetative, floral, and fruit characters. Leaflets in S. Mahagoni are generally smaller (mostly 4-6 cm long, 1.5-2.5 cm wide), petiolulate (especially the lower ones), and acute and sometimes aciculate (vs. mostly 7-9 cm long, 2-3 cm wide, subsessile, and long acuminate in S. humilis and mostly 9-13 cm long, 3-5 cm wide, petiolulate, and acute to short acuminate in S. macrophylla). Swietenia Mahagoni has the smallest capsules of the three species (4-6 cm long: vs. 8-16 cm in S. humilis and 12-15 cm in S. macrophylla) and also the smallest seeds. These are brown in contrast to the pale orange-brown seeds of S. humilis and the usually dark brown ones of S. macrophylla. The calyx and corolla are reported to be ciliate in S. Mahagoni and entire in S. humilis and S. macrophylla (Styles in Pennington, 1981, family references), but this difference was not apparent in numerous specimens of the three species that I studied. However, the flowers of S. humilis are slightly larger than those of the other two species (observations based on specimens in the combined herbaria of the Arnold Arboretum and Gray Herbarium). Although the diagnostic characteristics are largely quantitative and gradational, intermediates appear to be uncommon (except for the hybrids discussed earlier). Leaflet size and shape are variable in all three species, but especially so in S. Mahagoni, in which they can vary from two to four times longer than broad. Elliptic to ovate leaflets appear to be the commonest expression, although the shape is difficult to describe precisely because the laminae, and particularly the leaf bases, are asymmetrical, sometimes greatly so.

Swietenia and most other members of subfam. Swietenioideae have woody capsules containing a conspicuous columella and winged seeds. Species of *Swietenia* have ovoid woody capsules that open from the base to the apex (described by Johnson as starting in the middle of the capsule in *S. macrophylla*) and contain seeds with a large terminal wing, which is attached near the distal end of the columella. In *Khaya* A. Juss., the source of African mahogany and a genus thought by some (Lamb, 1966) to be close to *Swietenia*, the seeds have a complete, narrow marginal wing, and the capsules open from the apex to the base. Most other members of the tribe, except the poorly known *Schmardaea* Karsten, are restricted to the Old World.

Chromosome numbers vary within species (*Swietenia Mahagoni*, 2n = 12, 18, 24, 36, 42, 46–48, 54, 60, 108) and between species (*S. macrophylla*, 2n = 54 and *S. humilis*, 2n = 50, 52, 56; Datta & Samanta, Khosla & Styles,

Styles & Vosa). The euploid series in *S. Mahagoni* was documented in plantation trees (Fiji Islands), and an additional number (n = 28) has been reported for a tree grown in India (Sareen & Kumar). These numbers indicate the existence of considerable karyological polymorphism, at least in plantation stock. Khosla & Styles counted 2n = 48 (*S. macrophylla*), and 2n = 56 (*S. humilis*) in plants obtained from within the native ranges of the species. The chromosome cytology of the genus is otherwise poorly known, particularly within naturally established populations.

Few detailed studies of the morphology of species of Swietenia have been undertaken. Lee (1967) was the first to show that the flowers of S. Mahagoni and S. macrophylla were either staminate (styles long, ovaries slender) or carpellate (styles short, ovaries globose). The trees are monoecious. The number of staminate and carpellate flowers per inflorescence is reported to vary, with staminate flowers being more abundant. Observations of the same tree over two years showed a large difference in the number of carpellate flowers formed on an annual basis. Pollen is released in sticky masses suitable for transport by insects, which presumably are attracted to the nectariferous disc. Flowers of S. Mahagoni and S. macrophylla are reported to be fragrant (Small: Lamb. 1966). Only the undersurface of the stigma is receptive to pollen (Tomlinson). Dichogamy may be the rule in members of subfam. Swietenioideae, including Swietenia (Styles, family references), since the sparse field observations indicate that the central carpellate flower of a three-flowered dichasium opens first, followed by anthesis of the staminate flowers, which occur in a pair below the carpellate flower. This asynchrony may promote outcrossing, but the hybridizations performed by Lee (1968) indicate that in S. Mahagoni, at least, the trees are self-compatible. Usually only one carpellate flower per inflorescence develops into a mature fruit.

Growth of Swietenia Mahagoni follows a pattern similar to one typical of temperate trees, namely, articulate monopodial branching, scaly terminal bud formation, and suppression of secondary branches on primary shoots during the first year and release of the branches during the second year (Tomlinson). The xylem anatomy of the West Indian and Honduran mahoganies has been thoroughly characterized (Rock; under family references see Kribs; Panshin; Record, 1919, 1941, 1944). Annual growth increments are demarcated by bands of parenchyma. In comparison with the wood of Spanish cedar (Cedrela spp.), another economically important timber tree in the Meliaceae, intervascular pits in the mahoganies are smaller in diameter (2-3  $\mu$ m). In wood of the West Indian mahogany the perforation plates are simple, intervascular pitting of the vessel elements is alternate, pits of the fibers are simple and slitlike or vestigially bordered, and both apotracheal and paratracheal axial parenchyma are present, as are uniseriate and multiseriate heterocellular rays (Rock). Minute foliar nectaries occur on the petiole, rachis, petiolules, and both leaflet surfaces in all three species of Swietenia (Lersten & Rugenstein). Their positions in live plants are marked by minute glistening balls of nectar. Extrafloral nectaries such as these perhaps function to attract ants, which may help rid the plants of insect pests, a relationship demonstrated in other flowering plants. However, evidence for it in Swietenia is lacking.

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The seed biology of Swietenia is poorly documented. Seeds of S. macrophylla and probably those of the two other species have a short (several month) period of viability after ripening, unless the seeds are dried to five percent moisture content (Lamb, 1966). Viability is prolonged with refrigeration. The seeds have a prominent wing, and this structure presumably facilitates dispersal by wind, even though seedlings may be abundant under or near large trees. Lamb (1966) reported that seeds from a large tree of S. macrophylla can be scattered on the leeward side over an area of about 10 acres, but Johnson notes that seeds of this species are rarely found more than 100 yards from the parent tree. Capsules are borne erect in S. Mahagoni (and the other species). The seeds are weakly attached to the columella (central axis) and remain hanging loosely in place after the capsule valves have fallen away, which happens in the winter in Florida (C. E. Wood, Jr., obs.). Seeds are presumably dislodged by gusts of wind. Abundant aerenchymatous tissue occurs at the embryo end and in the wing along the raphe in seeds of S. humilis. It may increase the buoyancy of the seed in the air or possibly help to keep the seed floating in water. Aqueous leachates of leaves of S. Mahagoni inhibit the germination of its seeds in the laboratory (Andorfer & Teas), suggesting a possible allelopathic effect in nature. Seedlings of both S. Mahagoni and S. macrophylla are cryptocotylar. In the former the cophylls are alternate, whereas in S. macrophylla they are opposite (Duke, 1965).

Switenia Mahagoni was an important member of the highly diverse tropical hardwood forests that once were common in subtropical Florida (Craighead). Trees of the West Indian mahogany reaached a large size in hammocks (tree islands) that developed at places where the mineral soil or bedrock was slightly elevated (1 m or less) above the surrounding pinelands or glades (treeless wetlands). In such places fresh water remains year round in solution cavities and peat accumulates, both helping to maintain high humidity. West Indian mahogany was also common in a second kind of hammock that developed on ridges of marine marl deposited on the land by hurricane tides. Peat accumulation raised these low ridges further and isolated them from salt water. While charcoal preserved in the soil shows that fire swept through hammocks of both types, trees of *S. Mahagoni* can persist under such circumstances by forming root suckers.

Phoradendron rubrum (L.) Grisebach grows on Swietenia in some existing hammocks in Florida, and this parasite has been implicated in the death of larger trees on Key Largo and perhaps on Rhodes and Sand Keys (Cooley).

West Indian mahogany (Swietenia Mahagoni) and Honduran mahogany (S. macrophylla) are the sources of wood universally prized for cabinetry and fine woodworking for over 200 years. Honduran mahogany has been described as the "world's premier cabinet wood" and "perhaps the most valuable timber tree in the whole of tropical Latin America" (Styles in Pennington, 1981, family references; p. 400). Harvestable trees are still available in Mexico, Guatemala, and South America. West Indian mahogany is rare on the commercial market, and writing in the mid-1960's, Lamb commented that it had almost disappeared from commerce because the supply was exhausted. Its wood is thought to be superior to that of Honduran mahogany, which has a coarser grain and a less rich color when finished. Both mahoganies are presently being grown in forest plantations. Under natural conditions *S. macrophylla* is reported to reach 60 m tall; trees of *S. Mahagoni* are generally shorter (to 20 m).

The wood of Swietenia came to the attention of Europeans early in the 1500's during the Spanish domination of the West Indies. Over the next century and a half mahogany was used in the West Indics for shipbuilding and repair and in the construction of buildings because of its great resistance to dry rot and termites and to warping when in contact with water. Spanish shipbuilders, first at Santiago, Cuba, and later at Havana Arsenal, Cuba, constructed many ships for the Spanish Navy using logs cut in Cuba and Mexico (Lamb, 1966). The use of mahogany for furniture in England began about 1715. It rapidly supplanted walnut and oak as the raw material for tables, chairs, and cabinets, Lamb named the period 1725-1825 the "golden age of mahogany," in reference to the development of furniture styles during that 100 years by English master craftsmen, including Thomas Chippendale, George Hepplewhite, and Thomas Sheraton, who based their innovative designs on the strength, durability, outstanding working qualities, and excellent finished color and luster that are characteristic of mahogany. American cabinetmakers were also using mahogany in Boston, New York, Philadelphia, and elsewhere during this period. Especially prized were boards with highly patterned grain. These came from the stumps, root crowns, and larger roots, as well as from logs that included the junction of the bole and a large branch. Such logs were sawed so that the boards had a Y-shaped grain pattern.

Overharvesting has eliminated large trees of West Indian mahogany throughout its range, and what little of its wood comes on the market is from plantationgrown trees. Trees of Honduran mahogany are still available in parts of Central and South America. However, many of the largest trees have been cut from accessible locations. Concern has been expressed about the severe depletion of potentially useful genetic stock for breeding purposes (Styles in Pennington, 1981, family references). Mahogany shoot borers, *Hypsipyla* sp. (Lepidoptera), are scrious insect pests in many areas and have limited the development of mahogany plantations and the use of *Switetenia* species in reforestation projects (Styles & Khosla).

A decoction of the bark of *Swietenia Mahagoni* or of *S. macrophylla* has been used locally in the West Indies or Central America as a tonic and to treat inflamed mucous membranes and chest and other illnesses (Morton).

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